

JGR Biogeosciences

RESEARCH ARTICLE

10.1029/2018JG004849

Key Points:

- Traumatic resin ducts in the cross-dated tree rings of subalpine mountain hemlocks record tree damage during winter storms in Southeast Alaska
- Warmer, windier winters that accompany strong Aleutian Low pressure systems result in more tree damage
- Decadal-scale variability in North Pacific climate has impacted treeline ecosystems throughout this region

Supporting Information:

- Supporting Information S1

Correspondence to:

B. V. Gaglioti,
bengaglioti@gmail.com

Citation:

Gaglioti, B. V., Mann, D. H., Williams, A. P., Wiles, G. C., Stoffel, M., Oelkers, R., et al. (2019). Traumatic resin ducts in Alaska mountain hemlock trees provide a new proxy for winter storminess. *Journal of Geophysical Research: Biogeosciences*, 124, 1923–1938. <https://doi.org/10.1029/2018JG004849>

Received 2 OCT 2018

Accepted 16 APR 2019

Accepted article online 30 APR 2019

Published online 10 JUL 2019

Corrected 6 SEP 2019

This article was corrected on 6 SEP 2019. See the end of the full text for details.

Author Contributions:

Conceptualization: Benjamin V. Gaglioti

Data curation: Benjamin V. Gaglioti, Rose Oelkers, Benjamin M. Jones






Formal analysis: Benjamin V. Gaglioti, Rose Oelkers

Funding acquisition: Benjamin V. Gaglioti, Daniel H. Mann

Investigation: Benjamin V. Gaglioti, Daniel H. Mann, Gregory C. Wiles, Benjamin M. Jones

Methodology: Benjamin V. Gaglioti, Daniel H. Mann, A. Park Williams, (continued)

Traumatic Resin Ducts in Alaska Mountain Hemlock Trees Provide a New Proxy for Winter Storminess

Benjamin V. Gaglioti¹ , Daniel H. Mann², A. Park Williams¹ , Gregory C. Wiles³, Markus Stoffel^{4,5,6} , Rose Oelkers¹, Benjamin M. Jones⁷ , and Laia Andreu-Hayles¹ 

¹Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY, USA, ²Department of Geosciences, University of Alaska Fairbanks, Fairbanks, AK, USA, ³Department of Earth Sciences, The College of Wooster, Wooster, OH, USA, ⁴Institute for Environmental Sciences, University of Geneva, Geneva, Switzerland, ⁵Department of Earth Sciences, University of Geneva, Geneva, Switzerland, ⁶Department F.-A. Forel for Aquatic and Environmental Sciences, University of Geneva, Geneva, Switzerland, ⁷Water and Environmental Research Center, University of Alaska Fairbanks, Fairbanks, AK, USA

Abstract Winter is a critical season for land-surface feedbacks and ecosystem processes; however, most high-latitude paleo-environmental reconstructions are blind to cold season conditions. Here we introduce a winter-sensitive, paleo-proxy record that is based on the relative frequency of tangential rows of traumatic resin ducts (TRDs) in the annual growth rings of mountain hemlocks (*Tsuga mertensiana*) growing near treeline in Southeast Alaska. Hemlocks produce a row of TRDs in the earlywood portion of their annual rings in response to cambial damage incurred during winter. Multidecadal bouts of TRD production were followed by growth-leader replacement, reaction wood formation, and divergence in radial growth between storm-damaged trees and less exposed mountain hemlock forests. These patterns are consistent with TRDs being a response to tree damage caused by ice and snowstorms, a conclusion supported by the krummholz tree architecture at these sites. This relationship is further corroborated by significant correlations between our TRD record and the strength of the wintertime Aleutian Low (AL) pressure system that is linked to tree-damaging agents like wind, precipitation, and ice storm strength in Southeast Alaska. The combined TRD/krummholz architecture record indicates that abrupt shifts between strong and weak AL phases occurred every several decades since CE 1700 and that the 1800s had relatively long AL phases with heavy snowpacks. In addition to describing the magnitude and tempo of wintertime climate change in Northwestern North America, these results suggest that North Pacific Decadal Variability underlies the long-term dynamics of treeline ecosystems along the northeast Pacific coast.

1. Introduction

Winter conditions play a key role in many ecosystem processes at high latitudes and in some cases determine the range distributions of biota (Battisti et al., 2005; Hagedorn et al., 2014; Tape et al., 2010). Over recent decades in the Arctic and Subarctic, air temperature has been changing most rapidly in winter (Cohen et al., 2014; Walsh et al., 2011). To predict the future impacts of changing wintertime conditions, we need to know what winters were like before environmental record-keeping began, and how ecosystems responded to past changes in winter climate. At the same time, reconstructions of past wintertime conditions can provide valuable new insights into the historical climatology of ocean-atmospheric modes of variability that are primarily expressed during the Northern Hemisphere winter (i.e., the effects of the El Niño Southern Oscillation and North Pacific Decadal Variability; Trenberth & Hurrell, 1994; Wise & Dannenberg, 2014).

The wintertime states of low-pressure systems that develop over the North Pacific and North Atlantic Oceans affect climate and weather across vast, downwind regions (Hartmann, 2015). Prominent among these low-pressure systems is the Aleutian Low (AL), which is an important center of action for large-scale atmospheric circulation patterns (Rodionov et al., 2007). The strength and position of the AL affects the frequency, intensity, and trajectories of extratropical cyclones in the North Pacific (Mock et al., 1998; Rodionov et al., 2007; Trenberth & Hurrell, 1994; Zhu et al., 2007), as well as the state of climate teleconnections like the Pacific North American (PNA) pattern (Overland et al., 1999). Variations in the AL are described by the North Pacific Index (NPI), which is the mean sea level pressure within 30–65°N and 160°E–140°W (Figure 1; Trenberth & Hurrell, 1994). The strength of the AL strongly affects the

Gregory C. Wiles, Markus Stoffel, Rose Oelkers, Benjamin M. Jones, Laia Andreu-Hayles

Project administration: Benjamin V. Gaglioti

Resources: Benjamin V. Gaglioti, Gregory C. Wiles, Laia Andreu-Hayles

Supervision: Benjamin V. Gaglioti, Laia Andreu-Hayles

Validation: Benjamin V. Gaglioti

Visualization: Benjamin V. Gaglioti, A. Park Williams, Benjamin M. Jones, Laia Andreu-Hayles

Writing - original draft: Benjamin V. Gaglioti

Writing - review & editing:

Benjamin V. Gaglioti, Daniel H. Mann, Gregory C. Wiles, Markus Stoffel, Laia Andreu-Hayles

climate of Southeast Alaska, as indicated by negative correlations between the NPI and winter temperature, meridional winds, and, to a lesser extent, precipitation (stronger AL = higher temperatures, stronger winds, and more precipitation; Figure S1). These changes in the distribution and flux of southerly heat and wind energy advected into the North Pacific help drive the sea surface temperature anomaly patterns summarized by the Pacific Decadal Oscillation (PDO) index (Newman et al., 2016). At a larger spatial scale, the state of the AL affects droughts, floods, and wildfires in western North America (Cayan et al., 1998; Dannenberg & Wise, 2017; Seager et al., 2015; Wise, 2016); changes in earth-surface energy feedbacks like Arctic sea-ice extent (Rodionov et al., 2007); and the size and distribution of salmon runs along the Pacific coast (Mantua et al., 1997).

The sensitivity of North Pacific climate variability to forcing by greenhouse gas concentrations is a topic of widespread concern (i.e., Gan et al., 2017). However, separating ‘natural’ from anthropogenic drivers of change requires detailed, preindustrial records of past climate variability. A paleo-record estimating past variations of the AL can be very useful in this regard. Because the AL is most active in winter, finding paleo-records reflecting wintertime conditions is an important step forward for the investigation of the anthropogenic forcing on weather patterns. Unfortunately, records of wintertime conditions are rare in high-latitude regions.

Tree rings can provide detailed paleo-records of climate at annual, and in some cases, subannual temporal resolution (Hughes et al., 2010). However, high-latitude trees are dormant in winter and more sensitive to warm season conditions (Wilson et al., 2016). A winter-sensitive record requires a geographic setting that is exposed to extreme winter conditions and contains a tree species whose annual rings bear witness to conditions outside the growing season. One such place is alpine treeline. Trees there can be exposed to heavy snowpacks that affect growing season length and ring-width patterns (Körner, 2012; Peterson & Peterson, 2001). In addition, heavy snowpacks, ice abrasion, and rime-ice loading can damage plant tissue and cause stem or branch breakage, which in turn can affect tree growth rates, architecture, and wood morphology (Laberge et al., 2001; Pereg & Payette, 1998). Secular changes in tree architecture and growth rates of treeline trees have been used to reconstruct changing snow conditions and winter storminess during the Little Ice Age in Eastern Canada and elsewhere (Kajimoto et al., 2002; Laberge et al., 2001; Lavoie & Payette, 1992; Payette et al., 1989; Payette et al., 1994; Pereg & Payette, 1998; Tremblay & Bégin, 2005; Wooldridge et al., 1996).

Here we introduce a new dendrochronological proxy for winter conditions based on the anatomical features of cross-dated tree rings from mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) growing near altitudinal treeline in the coastal mountains of Southeast Alaska. This paleo-record reveals how wintertime tree-damaging events in the North Pacific region have varied since CE 1700 during the climate fluctuations that accompanied the Little Ice Age and post-industrial warming (Wiles et al., 2014).

2. Background: Tangential Rows of Traumatic Resin Ducts in Tree Rings

Conifers produce terpene-rich resins that serve as a physical and chemical defense against pathogens, insects, and decay (Zona, 2004). Taxa in the Pinaceae family respond to such threats by enhancing the xylematic production of resin ducts (Krokene et al., 2008), which are morphologically distinct cells that transport resin to areas of cambial damage (Bannan, 1936). Unlike the resin-rich Pinadeae subfamily, the Abietoideae subfamily, including *Tsuga* spp. (hemlocks), do not routinely invest in cambial resin-duct production (Bannan, 1936; Penhallow, 1907; Wu & Hu, 1997; Zona, 2004) and only produce tangential rows of what are termed traumatic resin ducts (TRDs) within ~50 vertical centimeters and ~80 radial degrees from a cambial wound (Bannan, 1934, 1936; Krokene et al., 2008; Schneuwly et al., 2009; Schneuwly et al., 2009). Transversely viewed, TRDs appear as thick-walled, lignified, vacuous, or pitch-filled vessels that occupy a portion or the entirety of individual tree rings (Figures 2c and 2d; Jeffrey, 1904; Penhallow, 1907; Bannan, 1936; Wu & Hu, 1997). The hormonal pathways that lead to resin duct production are initiated during the growing season a few days to weeks after damage occurs (Kuroda & Shimaji, 1983; Martin et al., 2002; Nagy et al., 2000) or at the onset of the following spring if the damage occurred prior to the growing season (Bannan, 1934; Fahn et al., 1979; Kuroda & Shimaji, 1983; Stoffel & Hitz, 2008; Zona, 2004). Resin ducts in the earlywood portion of the ring adjacent to the previous year's latewood indicate that damage occurred prior to or at the start of the growing season. In this way, the position of TRDs within an individual tree

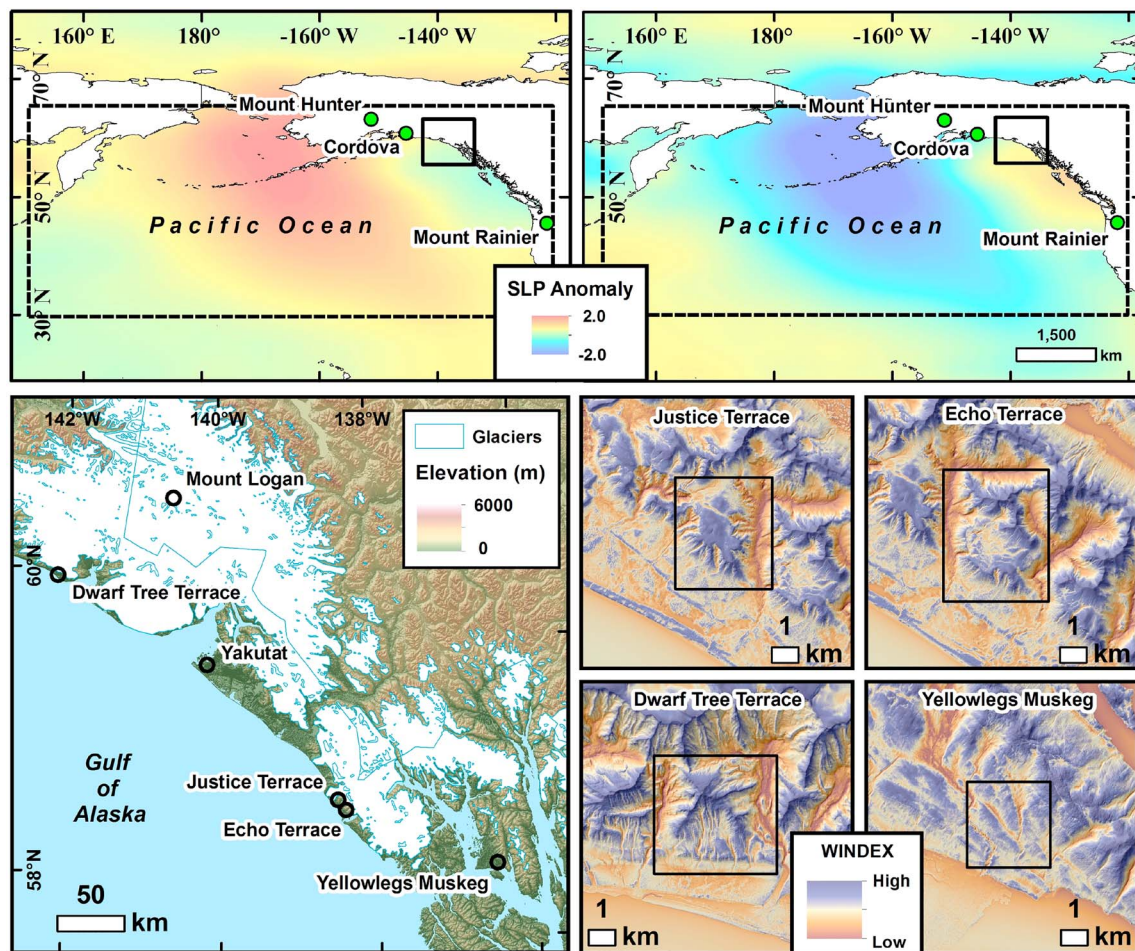


Figure 1. Top: The Northeast Pacific region showing locations mentioned in the text and mean winter (Nov-Mar) sea level pressure (SLP) anomaly patterns (Trenberth & Hurrell, 1994) during relatively weak (1948-1976; left) and strong (1977-2005; right) states of the Aleutian Low. Dashed box is the area where the North Pacific Index is calculated. Bottom left: Map of the Gulf of Alaska region with study sites. Bottom right: Topographic exposure index (WINDEX) is overlaid on the hillshade of the four storm-damaged tree sites (Boehner & Antonic, 2009; Gerlitz et al., 2015). Trees were sampled on flat, exposed terraces within each box.

ring can be used to reconstruct the seasonal timing of damage (Stoffel & Corona, 2014). Depending on the severity of the wound, proximity to cambial damage, and tree taxa, TRD production has been observed to persist for 1-3 years following injury (Kuroda & Shimaji, 1983; Nagy et al., 2000; Phillips & Croteau, 1999; Schneuwly, Stoffel, & Bollschweiler, 2009; Schneuwly, Stoffel, Dorren, & Berger, 2009; Stoffel & Hitz, 2008; Zona, 2004).

Previous studies have used the frequency and intra-ring position of TRDs to reconstruct long-term patterns of conifer tree damage from snow avalanches (Ballesteros-Cánovas et al., 2018; Butler & Sawyer, 2008; Casteller et al., 2007; Favillier et al., 2017; Schläppy et al., 2016; Stoffel et al., 2006; Stoffel & Hitz, 2008), rock-falls (Schneuwly, Stoffel, & Bollschweiler, 2009; Sorg et al., 2015; Stoffel et al., 2005; Stoffel & Perret, 2006), ice-damage or debris impacts due to flooding (Ballesteros et al., 2010; Lepage & Bégin, 1996; Zaginaev et al., 2016), other geomorphic disturbances (Stoffel, 2008; Stoffel & Bollschweiler, 2009), and bark beetle attacks (DeRose et al., 2017). We know of no study that has used TRDs to reconstruct winter storminess.

There are several mechanisms whereby intense winter storms can damage the cambium on the trunk of a tree. First, strain and shaking of the stem due to heavy winds and/or heavy snow and ice loads are known to cause damage to the cambial tissue anywhere along the stem (Fahn & Zamski, 1970; Gardiner et al., 2016). Second, ice abrasion from saltating ice crystals blowing across the snow surface can cause localized cambial damage (Holtmeier & Broll, 2010; Payette et al., 1994, 1996). Third, because well-spaced trees

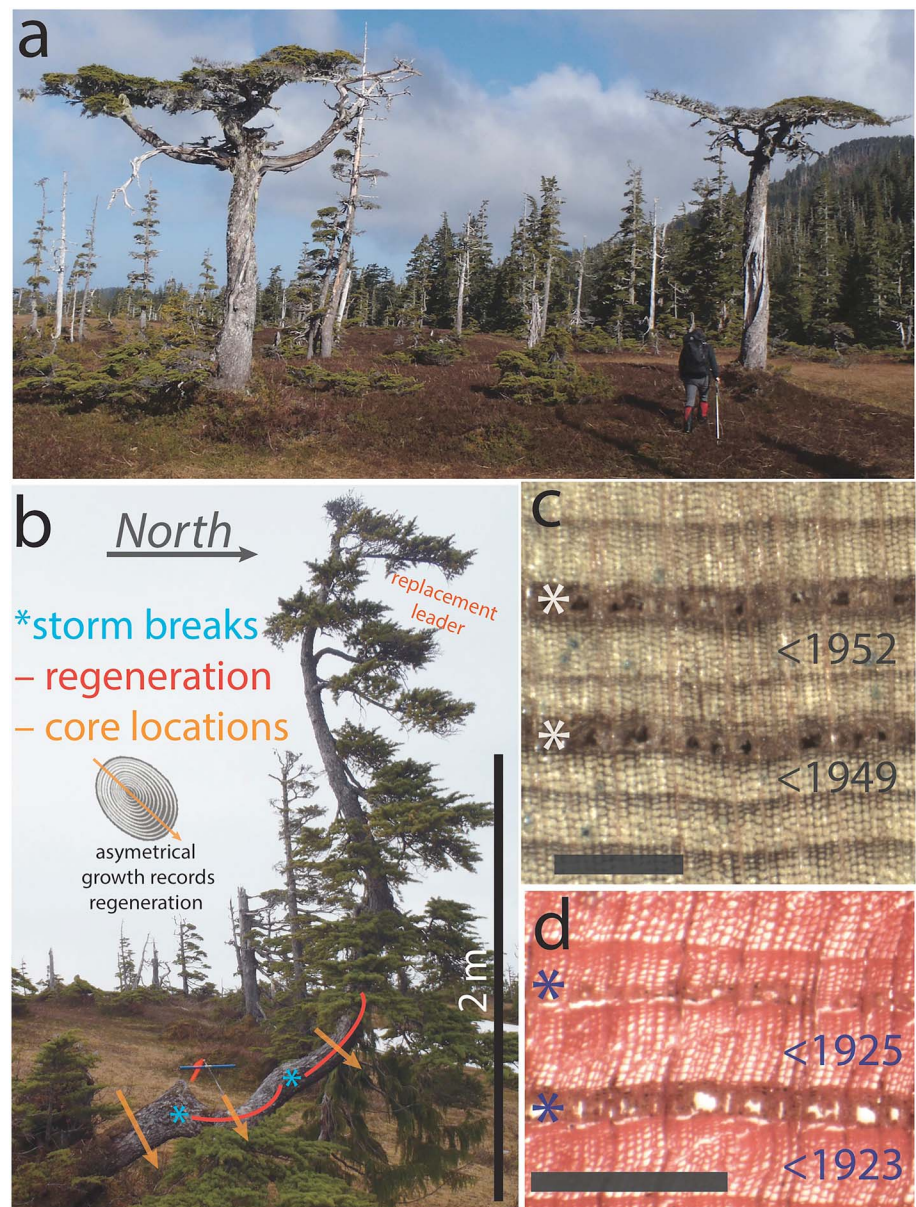


Figure 2. (a) Upright and (b) krummholz mountain hemlock trees growing near treeline at the Justice Terrace site. The changing morphology of krummholz trees record episodes of leader replacement by upturned branches following storm damage. (c) Photomicrograph of tangential rows of traumatic resin ducts (TRDs) marked with stars in cores taken near the base of upright trees. (d) Photomicrograph of TRDs in a thin-sectioned core marked with stars. Scale bars in c and d are 0.5 mm.

often have living foliage on lower branches that are prone to storm damage (Figures 2 and 3), TRD production in the lower stem could also reflect canopy damage in open forests (Bannan, 1936; Krokene et al., 2008).

3. Study Area

The sensitivity of this new proxy record relies on carefully choosing sampling locations where trees are chronically vulnerable to extreme winter conditions. We cored trees growing at three topographically exposed sites perched above the eastern Gulf of Alaska (Figure 1). Southeast Alaska is one of the

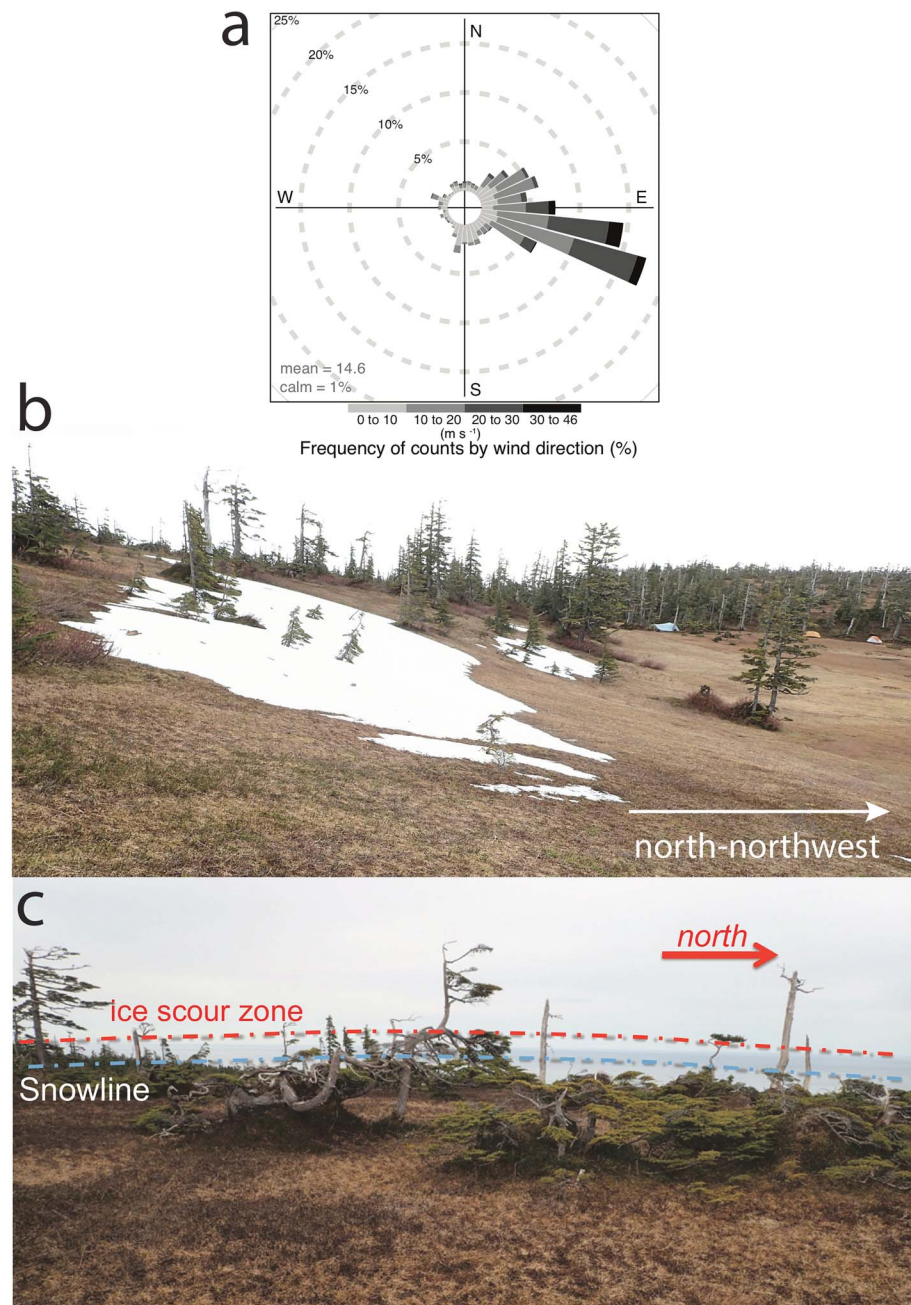


Figure 3. The architecture and distribution of subalpine mountain hemlocks at the study sites are dictated by winter weather. (a) Two-minute maximum of daily November-March wind speed and direction recorded at the Cordova, Alaska, airport (see Figure 1) between November 1999 and March 2017. (b) Justice Terrace site in mid-May 2017. The melting snowdrift covers much of this lee slope during the winter, and its persistence into the growing season excludes most trees. Lingering spring snow on north and northwest facing slopes is partly due to the prevailing winter winds from the southeast and partly due to reduced insolation. Blue and yellow tents seen in the background provide scale. (c) Krummholz trees on an exposed ridge at the Justice Terrace site are protected from wind and cold by the winter snowpack. During ice storm events, canopies projecting immediately above the snowpack are damaged by saltating ice particles and broken by loading under rime ice and snow. Branches and leaders above this ice scour zone are often leaning in the direction of the prevailing winter winds.

stormiest, high-latitude regions on Earth (Rodionov et al., 2007). (In the Aleut language, “Alaska” translates as ‘The object to where the action of the sea is directed’ (Orth, 1967)), At sea level in Yakutat, Alaska (Figure 1), an average of 2.24 m of precipitation falls annually between October and March (Arguez et al.,

2012), and winter storms often coincide with intense winds that cause frequent windthrow in forests (Nowacki & Kramer, 1998). Although there are no weather stations at our sites, which are located ~600 m above sea level (asl), snow and rain accumulation is assumed to be greater than at Yakutat; this inference is supported by the presence of 1- to 2-m-deep snowdrifts persisting into mid-May (Figure 3). Wintertime temperatures often fluctuate around freezing in Southeast Alaska at altitudes below 2,000 m asl (Buma et al., 2017), and these conditions are conducive to icing and heavy snow loads that are particularly harmful to trees and to human infrastructure (Chang et al., 2007; Irland, 2000; Nykänen et al., 1997).

The trees we sampled grow on uplifted marine terraces with paludified soils (Ugolini & Mann, 1979). The study stands consist of widely spaced, mountain hemlock trees, many of which are older than 400 years and possess complex growth forms indicative of repeated structural damage (Figures 2 and 3). Upright, relatively undisturbed trees growing on nearby well-drained slopes suggest that saturated soil conditions are the initial cause of these trees' diminutive stature. Soils consist of 5–10 cm of peat overlying a shallow B/C soil profile. Most trees grow outside the margins of late-lying snow-patches (Figure 3b). The result is a parkland-like, elfin forest in which individual trees are highly exposed to wind and to physical damage during extreme weather events (Irland, 2000; Stathers et al., 1994). Trees at these sites have minimal pathogen or insect damage, which is characteristically minor in mountain hemlocks (Means, 1990). The trees also show little sign of browsing from porcupines (*Erethizon dorsatum* L.).

Several field observations provide evidence that these growth-suppressed trees are strongly affected by winter weather. The topographic positions of snowdrifts and the asymmetrical tree morphology both reflect the predominance of southeasterly winds in winter (Figures 2b, 3, and S1). The umbel-style architecture of taller trees (>3 m in height) indicates repeated, height-dependent pruning of their canopies by the combined effects of wind and ice-crystal scouring, in addition to breakage by loading under rime ice and wet snow (Figure 2a). Another common growth form is a small- to medium-sized tree with numerous replacement leaders indicative of height-dependent, leader mortality (Figure 2b; Hibbs, 1981; Payette et al., 1989; Pereg & Payette, 1998). Elfin or krummholz trees (<3 m in height) growing on and near exposed ridgelines possess “snow skirts” of undamaged branches and foliage near their bases that indicate the presence of a protective snowpack (Figure 3; Payette et al., 1989). Directly above these skirts, many of these same trees have multiple leaders that are either killed or scarred by blowing ice crystals concentrated at the snow surface (Figure 3c). These observations suggest that tree architecture in the stands we studied is mainly a reflection of past winter conditions (i.e., Payette et al., 1996).

4. Methods

We collected 328 tree cores (0.5-cm diameter) from 117 subalpine mountain hemlock trees growing at three sites on the western flank of the Fairweather Range of the St. Elias Mountains in Southeast Alaska (Figure 1). To compare the rate of TRD production in these highly exposed forests with less exposed forests, we also collected 50 cores from 25 western hemlock trees (*Tsuga heterophylla*) growing in a lower elevation, less exposed forest (‘Yellowlegs’ in Figure 1). We cored trees within 1.5 m of their root crowns, and at least two cores per tree were taken 90° apart.

For the mountain hemlock trees, a subset of 34 krummholz trees were also cored through their replacement leaders, which are up-curved branches that take over the terminal growth position after an older leader is broken or damaged (Figure 2b). Together, the pith age and first episode of reaction wood in replacement leaders indicate when they took over the leader position (Figure 2b) and therefore provide a maximum-limiting age estimate for when previous leader mortality occurred. Pith ages of upright replacement leaders that persist for several decades to centuries indicate the onset of relatively heavy snowpacks that protects living tissue from ice scour. Subsequent episodes of reaction wood in replacement leaders were interpreted to indicate the occurrence of heavy winds, snow, and/or ice damage causing tree bending in the direction of prevailing winds (in this case southeasterly winds; Figures 2 and 3; Westing, 1965; Wade & Hewson, 1979; Schweingruber, 2012).

Tree cores were sanded with increasingly fine sand paper up to 1,000-grit to reveal ring boundaries, TRDs, and reaction wood. Ring widths were measured digitally to 0.001 mm using high-resolution scans and uploaded to the computer program Coorecorder 8.1. Ring-width series were visually and statistically cross-dated using standard dendrochronological techniques (Holmes, 1983; Stokes, 1996) to ensure that

each ring is assigned a calendar date (Table S1 in the supporting information). We detrended ring widths using a negative exponential curve and a 200-year spline curve to preserve age-independent tree-growth patterns related to the TRD record. The individual tree-ring indices were averaged using a robust mean, and this time series is hereafter referred to as the storm-damaged ring-width chronology (Cook, 1985).

We identified TRDs under 10-50x magnification as cells that were large, thick-walled, and dark compared to the surrounding tracheid cells that make up normal growth rings in *Tsuga* spp. (Figure 2; Schweingruber, 2007; Stoffel, 2008). The TRDs we observed were always arranged in one continuous tangential row and occupied ~10-100% of the annual ring (Figures 2c and 2d). We only counted those TRDs located along the earlywood ring boundary (~95% of the total TRDs) because this is the type of TRDs known to reflect winter trauma (Stoffel & Hitz, 2008). We identified reaction wood as being dark in color, having thick-walled tracheids, and having rings wider on the down-curve side than on the up-curve side of the same ring (Schweingruber, 2007).

Because taxa in the Abietoideae typically produce rows of TRDs within 1-3 years following physical damage (Bollschweiler et al., 2008), we used a 3-year bin of TRD occurrences in a tree for the index of annual winter storminess. For example, the TRD index from the year 1924 included all the TRDs observed in the 1924, 1925, and 1926 rings. Thus, the value for each tree for a single year can range from zero (no TRDs) to three (each of the three rings in a bin including t , $t+1$, and $t+2$ possessed TRDs). When a single year had multiple TRDs in the same tree but in different cores, we counted them as one TRD for that year. The final annual TRD record is the number of TRDs in that 3-year bin divided by the number of trees surveyed in those years (hereafter the TRD record). For example, if in the 1925 bin (rings representing 1925-1927), there were 10 total TRDs observed in the 100 trees surveyed for that year, then the TRD index was 10%.

To explore what climatic conditions drove TRD production in these treeline forests, we used Pearson's correlation coefficients between the TRD record (percent of trees growing early-wood TRDs) with various climate observations and indices from the same growth year. To determine whether the TRD record shared low frequency or decadal variability with climate indices, we used two methods: (1) cross-wavelet analysis following the methods of Torrence and Compo (1998). For this analysis, we detected coherent cycles in the TRD, PDO, and NPI time series at a 0.05 significance level for periods from 3-30 years. This test for coherence was passed when the average wavelet power between the two time series was outside the 95% range of a random simulation of 1,000 red noise time series with the same auto-regressive characteristics as the target time series. (2) Regime-shift detection analysis following the methods of Rodionov (2004). For this analysis we detected shifts in mean values using a cutoff value of 12 years (regimes that were <12 years required higher significant levels to identify a regime shift), a significance level of 0.1, and a Hubner's outlier weighting of two for both the TRD, PDO, and NPI time series. We then excluded regimes <8 years to avoid high-frequency variations affecting regime-shift identification.

We also assessed whether there was an age or ring-width bias in the rates of TRD production because such a bias would influence paleo-environmental reconstructions based on TRDs. We found that TRDs are less likely to occur in young trees (<300 years old). This pattern is contrary to the lowered TRD production rates in older trees observed in other conifers (Larson, 2012), and we think this is due to the younger trees at our study sites being smaller, less exposed, and protected by snow cover in winter. To compensate for this age effect, we adjusted TRD counts from relatively young trees by fitting a general additive model to a histogram of TRD occurrence organized by age into 20-year bins (Figure S2). We identified where the slope of this curve between two age bins was not significantly different from zero (non-zero slope ended at the 300- to 320-year age bin) and calculated the ratio between the probability density of each age bin less than 300 years to that occurring at 300 years. This ratio was then used as a multiplier to weight each TRD that occurred in a tree when it was <300 years old (Figure S2). To further assess this potential age bias in our final chronology, we calculated TRD records for trees when they were younger than 300 years and when they were older than 300 years.

Another potential source of bias is that wider annual rings may be more likely to contain TRDs. To check for this potential bias, we compared the distribution of raw ring widths and standardized ring widths of rings that had TRDs to those without TRDs using a Kolmogorov-Smirnov test (Lilliefors, 1967). We also tested whether aspect in relation to prevailing winds affected TRD occurrence within a tree by comparing rates of TRD occurrence in 59 south-facing (windward) cores with their north-facing counterparts from the

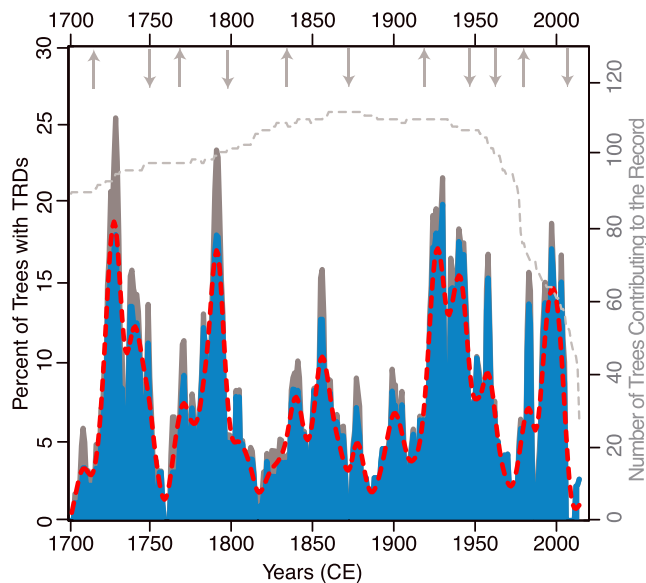


Figure 4. The relative frequency of traumatic resin ducts (TRDs; raw-percentages; blue polygon, age-weighted; gray polygon) in cross-dated tree rings from CE 1700 to 2014. The dashed gray line and right axis note the number of trees contributing to the record over time. The dashed red line is a smoothed spline with a 0.4 alpha smoothing parameter. Arrows at the top denote the timing and direction of regime shifts in the mean of the weighted TRD time series identified using Rodionov (2004) (significance level: 0.1; regime cutoff length: 12 years; Hubner's outlier weight parameter: 2).

same level of the same trunk and conducting a paired Student's *t*-test. Finally, to determine how tree-damaging episodes affected forest growth, we compared the ring-width indices of the storm-damaged trees from this study with the February-August air temperature reconstruction from the Gulf of Alaska region (Wiles et al., 2014), which is based on upright trees that experienced less storm damage. We used a 25-year running correlation between these two calendar-dated records to determine when storm-damaged trees were sensitive to the regional February-August air temperatures, and when they were insensitive to these interannual climate patterns. During times of low correlations, we infer that some other environmental factor besides February-August temperatures intervened to limit the growth of these storm-damaged trees.

5. Results and Discussion

5.1. The TRD Record

A 315-year TRD record (CE 1700–2014) was based on the relative frequency of TRDs at the three storm-exposed sites (Figure 4). Agreement between ring-width patterns was high among trees based on cross-dating statistics (Table S1), allowing us to confidently assign calendar dates to the TRD record. In general, multidecadal peaks of TRDs alternate with periods when relatively few trees produced TRDs (Figure 4). Overall, 0.88% of all rings surveyed in individual cores had early-wood TRDs (Table S2). The mean TRD index is 7% between CE 1700 and 2014 (Figure 4). This ranged from 0 to 25% of the trees surveyed (Figure 4). In a low-elevation, less exposed stand of western hemlock ('Yellowlegs' site in Figure 1 and Table S2), TRDs occur in trees at less than half the rate as

observed at the high-elevation sites (0.38% of all rings surveyed in individual cores). This provides further evidence that TRD production is not a random process in space and time, and, as is the case in related taxa (Stoffel, 2008), TRD production is triggered by damage to a tree's cambium, which occurred more frequently at the more exposed sites.

5.2. Distribution of TRDs Within Trees

Only 12% of TRDs were observed in the same 3-year bin somewhere else in the same tree. This suggests that mechanical damage in just a portion of the cambium is responsible for the presence of the TRDs. We found no bias in TRD orientation in north- versus south-facing cores from the same trees (*t*-test *p*-value 0.94), and no height-dependent bias in trees cored at different heights (Pearson's correlation between height a core was taken and percent of rings that had TRDs: $R = 0.05$). These patterns are consistent with prior observations that TRD production is localized within ~50 vertical centimeters and ~80 radial degrees of cambial damage in *Tsuga* spp. and other members of the Abietoideae (Bannan, 1934; Schneuwly, Stoffel, & Bollschweiler, 2009; Schneuwly, Stoffel, Dorren, et al., 2009). Because of this localized TRD occurrence, and our 2–6 cores per tree, it is possible that our cores missed some TRDs in certain trees. Nonetheless, our approach of randomly sampling this highly exposed forest allows us to gauge the relative rate of TRD production and tree damage over time.

We found that younger trees were less likely to be damaged and to produce TRDs than trees older than 300 years (Figure S2). As noted above, we correct for this bias by weighting TRD occurrence in trees when they were <300 years old. This age effect may arise because younger trees are short enough to be largely covered by the snowpack and hence protected from the elements through much of the winter (Kajimoto et al., 2002). Snow loading also inflicts less strain on younger trees because their smaller, more flexible branches can shed heavy snowfall (Marchand, 2014). This strain is known to drive cambial dieback at the base of the stem as well as near the canopy (Petty & Worrell, 1981; Spatz & Bruechert, 2000; Stokes, 1999). It is important to note that the main features of our TRD record do not change with or without this age-weighting (blue versus gray polygons in Figure 4), and the TRD record based on trees that are <300 years old is positively, albeit weakly,

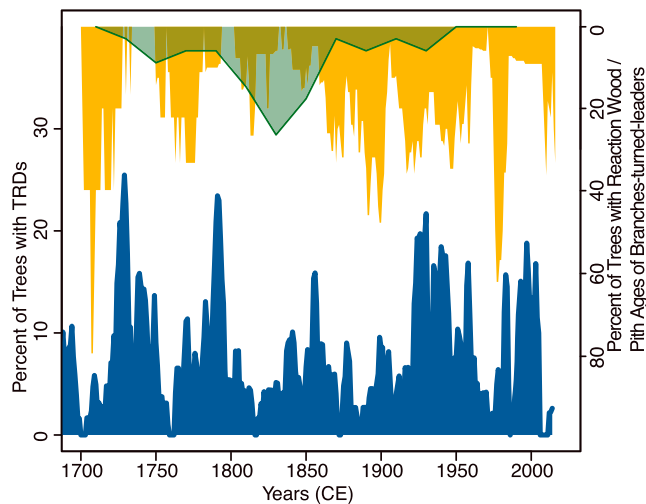


Figure 5. The alternating peaks of traumatic resin ducts (TRDs; blue), pith ages of replacement leaders (green), and reaction wood (orange) of replacement leaders ($n=38$; i.e., Figure 2) together form a consistent record of winter storm damage since CE 1700. TRDs record cambial damage during heavy ice storms. Pith ages on replacement leaders provide an age for when upturned branches grew upright and replaced a storm-damaged leader, probably during a time of deeper snowpack and lack of ice-storm damage. The timing of initial reaction wood in replacement leaders indicates when branches grew asymmetrically to regenerate into a leader. Reaction wood growth persists in leaders following damage from wind, snow, and ice coming from a predominant direction. In this case, asymmetrical growth was in response to southeasterly winds; Figures 2 and 3).

correlated with the record based solely on >300 -year-old trees ($R=0.33$; Figure S3). Therefore, the broad patterns of TRD production are not age dependent.

Results of Kolmogorov-Smirnov tests indicate that TRDs occur preferentially in growth rings that are relatively thin (Figure S4). However, after detrending ring width for tree age, the standardized ring widths of those rings containing TRDs are not significantly different from those without TRDs at the 95% confidence level (Figure S4). This suggests that TRD distribution is affected more by tree age than by ring width because raw ring widths are larger in younger trees because of age-related growth trends. We interpret this to mean that the occurrence of TRDs is not dependent on standardized ring width, which, in mountain hemlock trees in Southeast Alaska, is known to be sensitive to mean spring and summer temperatures (Wiles et al., 2014).

5.3. TRDs Compared With Other Tree Damage Indicators

We found that during periods with lower frequencies of TRDs, tree regeneration indicators, such as leader replacement and reaction wood, were more common in the studied trees. For instance, at the Justice Terrace site (Figure 1), high rates of replacement-leader recruitment occurred between CE 1810 and 1850 when relatively few trees generated TRDs (Figure 5). This period of new leader recruitment followed two prominent peaks in TRDs during the early and late 1700s and likely represents a deeper snowpack that provided protection while krummholz trees grew replacement leaders to relatively higher positions, which were then above the ice-scour zone in later years with thinner snowpacks. Similarly, more replacement leaders grew reaction wood during periods when relatively few trees laid down TRDs in their annual rings (Figure 5). The alternations of decades with heavy tree damage (i.e., TRDs) and enhanced tree

regeneration (i.e., leader replacement and reaction wood) is consistent with TRDs being an indicator of winter tree damage to treeline forests in Southeast Alaska.

In addition to the effects that winter weather had on tree damage, regeneration, and architecture at these treeline sites, tree-ring widths responded as well. The 25-year running correlation between the storm-damaged chronology and the February-August temperature reconstruction are insignificant ($R < 0.38$, p -value > 0.05) during the time when most replacement leaders began growing upright between 1810 and 1850 (Figure 6). The running correlations are also lower during some episodes when TRDs are more common (1720-1740, 1770-1785, 1900-1945, and after 1980; Figure 6). We hypothesize that (1) the enhanced snowpack that allowed a heightening of the krummholz tree canopy in the early 1800s caused ring-width patterns in the storm-damaged trees to diverge from temperature-sensitive tree-ring chronologies elsewhere in the region, and/or (2) enhanced leader damage in the 1700s caused the storm-damaged chronology to be less sensitive to climate during the initial phase of regeneration between CE 1810 and 1850.

Further corroborating the TRD and tree-architecture records, ring widths exhibit periods of declining growth during and immediately after some periods of peak TRD production (grey bands in Figure 6). This includes declining growth trends following TRD peaks in the 1720-1740s, 1780-1790s, 1920-1940s, and after the 1970s. We hypothesize that these growth deviations and/or lack of February-August temperature sensitivity reflect lowered resource allocation to radial growth as a result of (1) canopy damage that reduced the trees' photosynthetic capacity (Smith & Shortle, 2003) and/or (2) reduced radial growth due to the shifting of energy allocations to regeneration (i.e., reaction wood, wound healing, and root strengthening) and damage-reaction pathways (i.e., TRDs) following winters when storm damage was sustained (Zona, 2004). Similar growth-reduction deviations have been observed following ice storms in eastern North America (Hooper et al., 2001; Lafon & Speer, 2002; Smith & Shortle, 2003; Warrillow & Mou, 1999). Growth-reduction also occurred among treeline black spruce in Quebec after a reduction in snowpack depth during the Little Ice

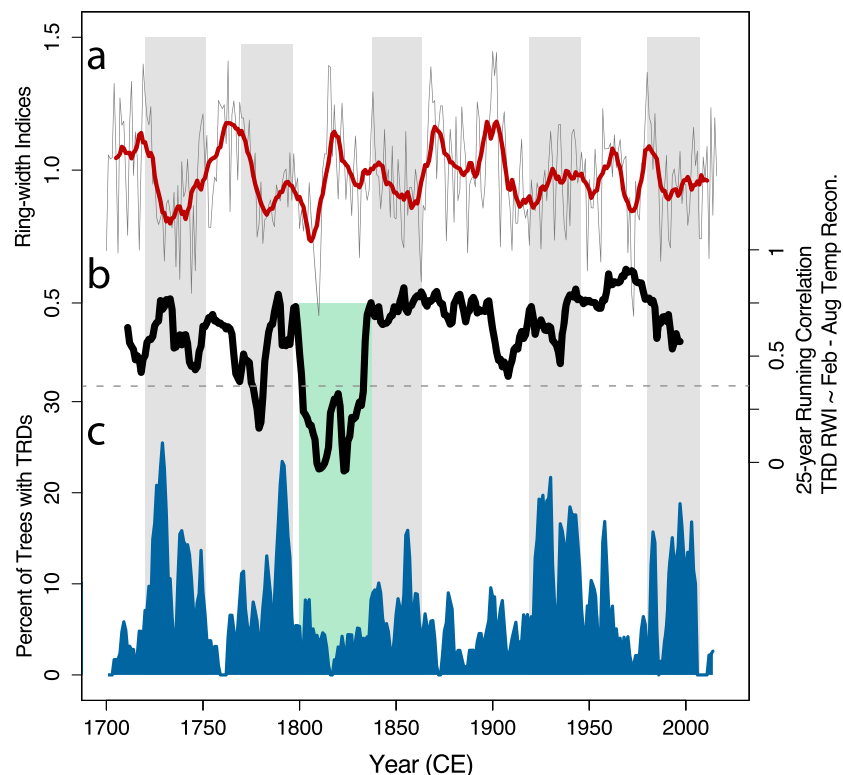


Figure 6. At these treeline sites, mountain hemlock's ability to prosper during warm springs and summers is compromised by damaging winter conditions. (a) Peaks of traumatic resin ducts (TRDs; see c, highlighted in gray) are followed by smaller ring-width indices in the 200-year spline detrended storm-damaged chronology (gray line; 10-year moving average: red line). (b) Twenty-five-year running correlations between the storm-damaged chronology and the regional February-August GOA temperature reconstruction (Wiles et al., 2014). Storm-damaged divergence is particularly dramatic between CE 1800 and 1850, when most of the krummholtz trees elevated their canopies, probably in response to the protection afforded by deeper snowpacks (Figure 5).

Age (Lavoie & Payette, 1992; Payette et al., 1989; Payette et al., 1994, 1996). Clearly, wintertime processes can have strong impacts on summertime growth processes in high-latitude forests.

In summary, our field observations and tree-ring data strongly suggest that changes in the abundance of TRDs in the annual rings of subalpine mountain hemlocks provide a dependable proxy record of the severity of past winter storm damage. The lines of evidence include the following: (1) more TRDs are found in trees growing in more topographically exposed sites; (2) bouts of heavy TRD production alternate with anatomical features associated with tree regeneration occurring during non-stormy times; (3) more TRDs are produced as trees get older, taller, and more exposed to wind, snow and ice damage; (4) radial growth rates and sensitivity to summertime climate sometimes decline after winters when TRD production indicates severe winter damage.

5.4. Climate Correlations

We have not used the TRD record to produce a quantitative reconstruction of climate, as is commonly done using ring-width indices (Hughes et al., 2010) in part because the TRD record consists of binary data (TRD presence/absence) in contrast to the continuous data derived from ring widths. Thus, each TRD episode represents the crossing of some threshold of physical damage that prompts a biological response in the tree. Thus, it is unlikely that the TRD record can be explained by any one climatic factor in a linear fashion. Nonetheless, by combining these binary measurements into a composite record of the percent of trees damaged in these stands, we can explore correlations with climate factors to reconstruct an informative, *qualitative* record of winter storminess near treeline in the study area.

Due to the remoteness of our study sites, we are relegated to comparing the TRD record with region-wide and reanalysis-based climate summary indices. The annual (3-year binned) TRD record is positively but weakly correlated with regional annual mean monthly winter temperatures and mean monthly meridional wind speeds (Figure S5). The annual TRD record also correlates significantly with instrumental data from Yakutat including the annual mean monthly temperatures from January to May ($R=0.36$; CE 1917–2014) and the annual number of winter (Nov–Mar) days with a daily mean above 0°C ($R=0.44$; CE 1948–2014). These climatic connections are logical because the likelihood for tree damage increases when winters are windier and when air temperatures are warmer, which in this case means near the freezing level (mean November–March air temperatures in Yakutat 1946–2017: -1.5°C ; 95% range: -5.3 to 2.2°C). Storms occurring when air temperatures are near freezing can be harmful to trees for several reasons: (1) Winter precipitation events that begin near 0°C followed by a cooling trend result in higher snow-loads on trees because warmer air masses hold more moisture and produce snow with higher moisture content (Schmidt & Gluns, 1991), which makes trees vulnerable to damage by straining branches and/or being damaged by subsequent wind events. (2) Warmer temperatures also make it more likely for winter ice storms to encase exposed branches and foliage in rime ice, which is one of the main forest disturbance agents in regions where winter temperatures fluctuate around the freezing point (Changnon, 2003). (3) A higher density of rime ice is deposited when temperatures are near freezing, whereas less adherent, soft rime is deposited at temperatures $< -8^{\circ}\text{C}$ (Baranowski & Liebersbach, 1977; Makkonen, 2000). In summary, warmer winters in Southeast Alaska make tree-damaging events more likely to occur, and this is reflected in the TRD record.

5.5. Tree Damage Is Related to Shifts in the North Pacific Climate Indices

Based on the likelihood that a combination of climate variables underlie tree damage at our study sites, we explored the relationship between large-scale climate indices and the TRD record. Climate summaries like the wintertime NPI and PDO are often correlated with many of the climatic variables relevant for tree damage in Southeast Alaska (temperature, wind, and precipitation; Figure S1; Trenberth & Hurrell, 1994). Based on the changing frequency of TRDs, the trees we studied had a higher likelihood of being physically damaged during synoptic conditions associated with a relatively strong AL (Figure 7; negative NPI; annual November–March NPI–TRD record: $R = -0.34$; CE 1900–2014) and a relatively positive PDO pattern (Figure S6; annual December–May PDO–TRD record: $R=0.41$; CE 1900–2014). As a result, during springs following strong AL (negative NPI) and positive PDO winters, more subalpine mountain hemlock trees responded to the stress and damage of severe winter weather by producing TRDs than during springs following winters with a comparatively weak AL (positive NPI) and negative PDO (Figure 7). This connection makes sense because (1) weather-station data show that a strong AL and a positive PDO are accompanied by warmer, windier, and rainier winters in Southeast Alaska (Mock et al., 1998; Neal et al., 2002) and (2) the TRD record has a similar multidecadal phasing as the AL and PDO (Figure 7). In support of this, average cross-wavelet analysis of the annual TRD record and the wintertime NPI/PDO had a significant power in the 16- to 21-year frequency (Figure S7). In addition, most of the regime shifts identified in the NPI and PDO records were within 4 years as those identified in the TRD record (Figure 7). Overall, decadal bouts of heavy TRD production in prehistoric times coincided with decades when the AL was stronger and the PDO was positive.

If the relationship between TRD production and these regional ocean-atmospheric modes of variability is stationary, we can conclude that the bimodal, multidecadal AL/PDO regimes that are prominent in the post-CE 1900 instrumental period have occurred throughout the entire TRD record from CE 1700 to 2014 (Figure 4). We can also conclude that the twentieth century had a similar tempo and magnitude of storm damage as the eighteenth century (Figure 4), while in contrast, the nineteenth century had longer, more variable episodes of tree damage and regeneration representing shifts in the NPI/PDO (Figures 4 and 5). A particularly interesting time period for NPI/PDO dynamics was between CE 1800 and 1850, when the krummholz canopy rose, and ring widths in storm-damaged trees diverged markedly from their temperature-sensitive counterparts, which may represent a particularly weak AL phase (low TRD numbers), and the beginning of a multidecadal episode with heavy winter snowpacks (Figure 6).

5.6. Comparison With Other Records of Regional Climate

Paleo-reconstructions of North American teleconnection patterns and water resources governed by the AL generally agree with the temporal pattern of tree damage recorded by TRDs since CE 1700. First,

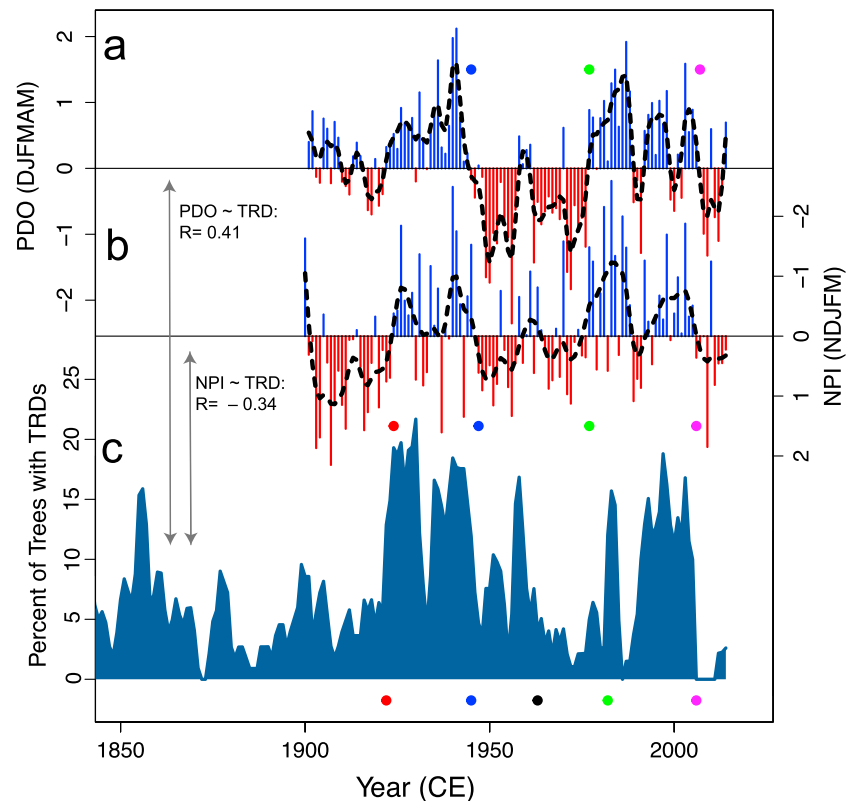


Figure 7. Rates of traumatic resin duct (TRD) production in treeline forests of Southeast Alaska (panel c) are related to winter climate indices in the North Pacific region. (a) December-May mean Pacific Decadal Oscillation (PDO) index. (b) November-March North Pacific Index (NPI; Aleutian Low index; AL; note inverse values in y-axis). Correlations ($R=$) are Pearson's correlation coefficients between the climate indices and the annual TRD record. Winters with stronger Aleutian Lows and more positive PDOs are accompanied by more tree damage. The dots represent the timing of regime shifts for each time series based on Rodionov (2004). The same dot colors indicate a shared timing of regime shifts between TRDs and climate indices, where “shared” means they occurred within 4 years of each other, and shift in the same direction. The black dot represents a regime shift detected in the TRD time series that was not detected in the either the PDO or NPI time series.

correlations between the annual TRD record and the annual February–August mean temperature reconstruction based on mountain hemlocks in the Gulf of Alaska sites are significant (Figure 6; $R=0.39$; CE 1700–2010; Wiles et al., 2014). In addition, the annual TRD record is weakly correlated ($R=0.27$) with a tree ring- and varved lake-sediment-based reconstruction of the wintertime PNA that integrates far afield proxy records from the American Southwest and New England (Liu et al., 2017). This is expected because a more positive PNA pattern in the instrumental record is associated with a stronger AL (Overland et al., 1999) and thus with more tree damage in Southeast Alaska. Also, as expected from the contrasting influences of AL intensity on winter storminess between Southeast Alaska and the Pacific Northwest (Washington and Oregon), the low-frequency TRD record corresponds well with the low-frequency growth variability among trees at high-elevation sites in Washington and Oregon where growth rates are limited by the amount of spring snowpack (Figure S8; Peterson & Peterson, 2001). Overall, these far-afield correlations suggest that because of being affected by past shifts in the AL and PDO, the TRD record has implications for cold season moisture variability across large regions of downwind North America.

In contrast, the Wise and Dannenberg (2014) reconstruction of the cold season 500-mb height field over the North Pacific shows poor agreement with our TRD record. This could be due to varying seasonal sensitivities of the tree-ring chronologies or because of the lack of tree-ring data from sites above $\sim 50^\circ\text{N}$ in their reconstruction. In addition, the TRD record does not indicate a multicentury strengthening of the AL since the mid-eighteenth century as is inferred from the Mount Hunter and Mount Logan ice cores (Osterberg et al., 2017; Winski et al., 2017; Figures 4 and 5), but this could be because we do not have a pre-1700 TRD period for comparison.

5.7. Impacts of Climate Change on Treeline Forests in Southeastern Alaska

The dynamics of alpine treelines are often governed by changes in the climatic variables that control the upper limits of tree growth and tree-seedling establishment (Körner, 2012). In general terms, changes in summer temperatures are often invoked as the drivers of ecological changes at treeline; an interpretation supported by treeline expansion during warm periods in the early Holocene (MacDonald et al., 2000; Mann et al., 2010), the Medieval Warm Period (Hiller et al., 2001), and the twentieth century (Kullman & Öberg, 2009). But how does treeline behave in hypermaritime locations where long-term climatic trends have been minor relative to the decadal climatic variability associated with ocean-atmospheric regime shifts (Wendler et al., 2016)? For example, frequent multidecadal shifts and cycles of winter climate in the coastal regions of Southeast Alaska can create more complicated dynamics for treeline responses than simpler, directional trends in summer air temperatures. In our study area, a strong phase of the AL that persists for several decades may enhance tree damage and compromise growth and recruitment in highly exposed forests. On the contrary, more protected treeline sites that make up most of the dendroclimatology record in this region tend to respond to this same strong AL phase with favorable growth and perhaps forest expansion as a result of warmer springs and summers (Wiles et al., 2014; Wilson et al., 2007). We hypothesize that in addition to monotonic climate change, the nature of these decadal-scale shifts in climate has been a primary driver in past treeline dynamics in the hyper-oceanic regions of Northwestern North America.

6. Conclusions

Most high-latitude, paleo-climate proxies are blind to wintertime conditions. The relative frequency of TRDs formed in subalpine mountain hemlocks growing in hypermaritime, treeline stands in Southeast Alaska provides a record of tree damage during winter. TRDs record local cambial damage in response to heavy wind damage and/or ice scour on tree stems and branches. TRDs were less likely to occur when trees are younger, smaller, and protected under the snowpack during winter. At the sites we studied, there is no apparent ring width, height, or aspect bias for TRD occurrence. Radial growth rates in storm-damaged forests diverged from growth rates in more protected mountain hemlock forests during episodes of increased TRD production and inferred heavy snowpacks, suggesting that winter processes can also affect forest productivity at these treeline sites. During winters when the AL pressure system is particularly strong, warmer temperatures and enhanced southerly winds create icy, stormy conditions that increase the likelihood of tree damage and TRD production. This paleo-environmental perspective on the strength of the AL and the phase of the PDO indicates that the bimodal patterns of North Pacific Decadal Variability known from the post-1900 instrumental record also occurred back to at least CE 1700. We hypothesize that these shifts in wintertime climate may be a primary driver of treeline dynamics along the North Pacific coastline. This new tree-ring proxy provides a measure of winter storminess that can be applied to other synoptic patterns or weather events where similar tree taxa produce TRDs in response to extreme weather events.

References

- Arguez, A., Durre, I., Applequist, S., Vose, R. S., Squires, M. F., Yin, X., et al. (2012). NOAA's 1981–2010 US climate normals: An overview. *Bulletin of the American Meteorological Society*, 93(11), 1687–1697. <https://doi.org/10.1175/BAMS-D-11-00197.1>
- Ballesteros, J. A., Stoffel, M., Bodoque, J. M., Bollschweiler, M., Hitz, O., & Diez-Herrero, A. (2010). Changes in wood anatomy in tree rings of *Pinus pinaster* Ait. following wounding by flash floods. *Tree-Ring Research*, 66(2), 93–103. <https://doi.org/10.3959/2009-4.1>
- Ballesteros-Cánovas, J. A., Trappmann, D., Madrigal-González, J., Eckert, N., & Stoffel, M. (2018). Climate warming enhances snow avalanche risk in the Western Himalayas. *Proceedings of the National Academy of Sciences*, 115(13), 3410–3415. <https://doi.org/10.1073/pnas.1716913115>
- Bannan, M. W. (1934). Seasonal wounding and resin-cyst production in the hemlock, *Tsuga canadensis* (L.) Carr. *Annals of Botany*, 48(192), 857–868.
- Bannan, M. W. (1936). Vertical resin ducts in the secondary wood of the Abietineae. *New Phytologist*, 35(1), 11–46. <https://doi.org/10.1111/j.1469-8137.1936.tb06864.x>
- Baranowski, S., & Liebersbach, J. (1977). The intensity of different kinds of rime on the upper tree line in the Sudety Mountains. *Journal of Glaciology*, 19(81), 489–497.
- Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A., & Larsson, S. (2005). Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological applications*, 15(6), 2084–2096. <https://doi.org/10.1890/04-1903>
- Boehner, J., & Antonic, O. (2009). Land Surface Parameters Specific to Topo-Climatology. In T. Hengl & H. I. Reuter (Eds.). *Geomorphometry: Concepts, Software, Applications* (pp. 195–226).
- Bollschweiler, M., Stoffel, M., Schneuwly, D. M., & Bourqui, K. (2008). Traumatic resin ducts in *Larix decidua* stems impacted by debris flows. *Tree Physiology*, 28(2), 255–263. <https://doi.org/10.1093/treephys/28.2.255>

Acknowledgments

All instrumental and reanalysis climate data presented here were downloaded from <https://climexp.knmi.nl/>. All paleoenvironmental data that were compared with the data presented here were downloaded from <https://www.ncdc.noaa.gov/data-access/paleoclimatology-data>. New data generated by this study and presented in this paper including the tree ring-width records, TRD frequency, and reaction wood frequency can be found in the supplemental material of this manuscript and will eventually be available in the noaa.gov paleoclimatology data set. This work was funded by the Climate Center at Lamont-Doherty Earth Observatory (LDEO) at Columbia University as well as the National Park Service. The LDEO Postdoctoral Fellowship funded BVG's time. D. H. M., A. P. W., G. C. W., and L. A. H. received funding from the National Science Foundation (OPP-1203271, AGS-1703029, AGS-1502186, PLR-1504134, AGS-1502150, OISE-1743738, and PLR-1603473). We thank Rowan Sharman, Philip Wilson, and Virgil E. Purchase for help in the field and Kyle Hansen for lab assistance. This project benefitted from expert piloting by Gary Thompson of Admiralty Air and logistical support by Lewis Sharman. Discussions with Greg Streveler, Bruce Finney, Alexey Kaplan, Edward Cook, and Brendan Buckley contributed to our thinking on this project. We acknowledge the pioneering tree ring work of Gordon Jacoby who collected the samples at the 'Dwarf Trees' site during a no-doubt stormy November in 1979. This is LDEO contribution #8327.

- Buma, B., Hennon, P. E., Harrington, C. A., Popkin, J. R., Krapek, J., Lamb, M. S., et al. (2017). Emerging climate-driven disturbance processes: Widespread mortality associated with snow-to-rain transitions across 10° of latitude and half the range of a climate-threatened conifer. *Global Change Biology*, 23(7), 2903–2914. <https://doi.org/10.1111/gcb.13555>
- Butler, D. R., & Sawyer, C. F. (2008). Dendrogeomorphology and high-magnitude snow avalanches: A review and case study. *Natural Hazards and Earth System Science*, 8(2), 303–309. <https://doi.org/10.5194/nhess-8-303-2008>
- Casteller, A., Stöckli, V., Villalba, R., & Mayer, A. C. (2007). An evaluation of dendroecological indicators of snow avalanches in the Swiss Alps. *Arctic, Antarctic, and Alpine Research*, 39(2), 218–228. [https://doi.org/10.1657/1523-0430\(2007\)39\[218:AEODIO\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2007)39[218:AEODIO]2.0.CO;2)
- Cayan, D. R., Dettinger, M. D., Diaz, H. F., & Graham, N. E. (1998). Decadal variability of precipitation over western North America. *Journal of Climate*, 11(12), 3148–3166. [https://doi.org/10.1175/1520-0442\(1998\)011<3148:DVOPOW>2.0.CO;2](https://doi.org/10.1175/1520-0442(1998)011<3148:DVOPOW>2.0.CO;2)
- Chang, S. E., McDaniels, T. L., Mikawoz, J., & Peterson, K. (2007). Infrastructure failure interdependencies in extreme events: Power outage consequences in the 1998 Ice Storm. *Natural Hazards*, 41(2), 337–358. <https://doi.org/10.1007/s11069-006-9039-4>
- Changnon, S. A. (2003). Characteristics of ice storms in the United States. *Journal of Applied Meteorology*, 42(5), 630–639. [https://doi.org/10.1175/1520-0450\(2003\)042<0630:COISIT>2.0.CO;2](https://doi.org/10.1175/1520-0450(2003)042<0630:COISIT>2.0.CO;2)
- Cohen, J., Screen, J. A., Furtado, J. C., Barlow, M., Whittleston, D., Coumou, D., et al. (2014). Recent Arctic amplification and extreme mid-latitude weather. *Nature Geoscience*, 7(9), 627–637. <https://doi.org/10.1038/ngeo2234>
- Cook, E. R. (1985). A time series analysis approach to tree ring standardization (dendrochronology, forestry, dendroclimatology, autoregressive process). PhD Dissertation, University of Arizona
- Dannenberg, M. P., & Wise, E. K. (2017). Shifting Pacific storm tracks as stressors to ecosystems of western North America. *Global Change Biology*, 23(11), 4896–4906. <https://doi.org/10.1111/gcb.13748>
- DeRose, R. J., Bekker, M. F., & Long, J. N. (2017). Traumatic resin ducts as indicators of bark beetle outbreaks. *Canadian Journal of Forest Research*, 47(9), 1168–1174. <https://doi.org/10.1139/cjfr-2017-0097>
- Fahn, A., Werker, E., & Ben Tzur, P. (1979). Seasonal effects of wounding and growth substances on development of traumatic resin ducts in Cedrus libani. *New Phytologist*, 82(2), 537–544. <https://doi.org/10.1111/j.1469-8137.1979.tb02680.x>
- Fahn, A., & Zamski, E. (1970). The influence of pressure, wind, wounding and growth substances on the rate of resin duct formation in Pinus halepensis wood. *Israel Journal of Botany*, 19(2/3), 429–446.
- Favillier, A., Guillet, S., Morel, P., Corona, C., Saez, J. L., Eckert, N., et al. (2017). Disentangling the impacts of exogenous disturbances on forest stands to assess multi-centennial tree-ring reconstructions of avalanche activity in the upper Goms Valley (Canton of Valais, Switzerland). *Quaternary Geochronology*, 42, 89–104. <https://doi.org/10.1016/j.quageo.2017.09.001>
- Gan, B., Wu, L., Jia, F., Li, S., Cai, W., Nakamura, H., et al. (2017). On the response of the Aleutian low to greenhouse warming. *Journal of Climate*, 30(10), 3907–3925. <https://doi.org/10.1175/JCLI-D-15-0789.1>
- Gardiner, B., Berry, P., & Moulia, B. (2016). Wind impacts on plant growth, mechanics and damage. *Plant Science*, 245, 94–118. <https://doi.org/10.1016/j.plantsci.2016.01.006>
- Gerlitz, L., Conrad, O., & Böhner, J. (2015). Large-scale atmospheric forcing and topographic modification of precipitation rates over High Asia—a neural-network-based approach. *Earth System Dynamics*, 6(1), 61.
- Hagedorn, F., Shiyatov, S. G., Mazepa, V. S., Devi, N. M., Grigor'ev, A. A., Bartysh, A. A., et al. (2014). Treeline advances along the Urals mountain range—driven by improved winter conditions? *Global Change Biology*, 20(11), 3530–3543. <https://doi.org/10.1111/gcb.12613>
- Hartmann, D. L. (2015). *Global physical climatology*. Newnes.
- Hibbs, D. E. (1981). Leader growth and the architecture of three North American hemlocks. *Canadian Journal of Botany*, 59(4), 476–480. <https://doi.org/10.1139/b81-066>
- Hiller, A., Boettger, T., & Kremenetski, C. (2001). Mediaeval climatic warming recorded by radiocarbon dated alpine tree-line shift on the Kola Peninsula, Russia. *The Holocene*, 11(4), 491–497. <https://doi.org/10.1191/095968301678302931>
- Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement, Tree-ring bulletin
- Holtmeier, F.-K., & Broll, G. (2010). Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic. *Physical Geography*, 31(3), 203–233. <https://doi.org/10.2747/0272-3646.31.3.203>
- Hooper, M. C., Arai, K., & Lechowicz, M. J. (2001). Impact of a major ice storm on an old-growth hardwood forest. *Canadian Journal of Botany*, 79(1), 70–75.
- Hughes, M. K., Swetnam, T. W., & Diaz, H. F. (2010). *Dendroclimatology: Progress and prospects*. Springer Science and Business Media.
- Irland, L. C. (2000). Ice storms and forest impacts. *Science of the total environment*, 262(3), 231–242. [https://doi.org/10.1016/S0048-9697\(00\)00525-8](https://doi.org/10.1016/S0048-9697(00)00525-8)
- Jeffrey, E. C. (1904). The comparative anatomy of the Coniferales II. The Abietineae. *Memoirs read before the Boston Society of Natural History*, 6, 1–37.
- Kajimoto, T., Seki, T., Ikeda, S., Daimaru, H., Okamoto, T., & Onodera, H. (2002). Effects of snowfall fluctuation on tree growth and establishment of subalpine Abies mariesii near upper forest-limit of Mt. Yumori, northern Japan. *Arctic, Antarctic, and Alpine Research*, 34(2), 191–200. <https://doi.org/10.1080/15230430.2002.12003484>
- Körner, C. (2012). *Alpine treelines: Functional ecology of the global high elevation tree limits*. Springer Science and Business Media. <https://doi.org/10.1007/978-3-0348-0396-0>
- Krokene, P., Nagy, N. E., & Krekling, T. (2008). Traumatic resin ducts and polyphenolic parenchyma cells in conifers, (pp. 147–169).
- Kullman, L., & Öberg, L. (2009). Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: A landscape ecological perspective. *Journal of Ecology*, 97(3), 415–429. <https://doi.org/10.1111/j.1365-2745.2009.01488.x>
- Kuroda, K., & Shimaji, K. (1983). Traumatic resin canal formation as a marker of xylem growth. *Forest Science*, 29(3), 653–659.
- Laberge, M.-J., Payette, S., & Pitre, N. (2001). Development of stunted black spruce (Picea mariana) clones in the subarctic environment: A dendroarchitectural analysis. *Ecoscience*, 8(4), 489–498. <https://doi.org/10.1080/11956860.2001.11682679>
- Lafon, C. W., & Speer, J. H. (2002). Using dendrochronology to identify major ice storm events in oak forests of southwestern Virginia. *Climate Research*, 20(1), 41–54. <https://doi.org/10.3354/cr020041>
- Larson, P. R. (2012). *The vascular cambium: Development and structure*. Spring Science and Business Media.
- Lavoie, C., & Payette, S. (1992). Black spruce growth forms as a record of a changing winter environment at treeline, Quebec, Canada. *Arctic and Alpine Research*, 24(1), 40–49. <https://doi.org/10.2307/1551318>
- Lepage, H., & Bégin, Y. (1996). Tree-ring dating of extreme water level events at Lake Bienville, Subarctic Québec, Canada. *Arctic and Alpine Research*, 28(1), 77–84. <https://doi.org/10.2307/1552088>
- Lilliefors, H. W. (1967). On the Kolmogorov-Smirnov test for normality with mean and variance unknown. *Journal of the American statistical Association*, 62(318), 399–402. <https://doi.org/10.1080/01621459.1967.10482916>

- Liu, Z., Tang, Y., Jian, Z., Poulsen, C. J., Welker, J. M., & Bowen, G. J. (2017). Pacific North American circulation pattern links external forcing and North American hydroclimatic change over the past millennium. *Proceedings of the National Academy of Sciences*, 114(13), 3340–3345. <https://doi.org/10.1073/pnas.1618201114>
- MacDonald, G. M., Velichko, A. A., Kremenetski, C. V., Borisova, O. K., Goleva, A. A., Andreev, A. A., et al. (2000). Holocene treeline history and climate change across northern Eurasia. *Quaternary Research*, 53(03), 302–311. <https://doi.org/10.1006/qres.1999.2123>
- Makkonen, L. (2000). Models for the growth of rime, glaze, icicles and wet snow on structures. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences*, 358(1776), 2913–2939. <https://doi.org/10.1098/rsta.2000.0690>
- Mann, D. H., Groves, P., Reanier, R. E., & Kunz, M. L. (2010). Floodplains, permafrost, cottonwood trees, and peat: What happened the last time climate warmed suddenly in arctic Alaska? *Quaternary Science Reviews*, 29(27–28), 3812–3830. <https://doi.org/10.1016/j.quascirev.2010.09.002>
- Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78(6), 1069–1079. [https://doi.org/10.1175/1520-0477\(1997\)078<1069:APICOW>2.0.CO;2](https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2)
- Marchand, P. J. (2014). *Life in the cold: An introduction to winter ecology*. UPNE.
- Martin, D., Tholl, D., Gershenzon, J., & Bohlmann, J. (2002). Methyl jasmonate induces traumatic resin ducts, terpenoid resin biosynthesis, and terpenoid accumulation in developing xylem of Norway spruce stems. *Plant physiology*, 129(3), 1003–1018. <https://doi.org/10.1104/pp.011001>
- Means, J. E. (1990). *Tsuga mertensiana* (Bong.) Carr, *Mountain hemlock*. *Silvics of North America*, 1, 623–631.
- Mock, C. J., Bartlein, P. J., & Anderson, P. M. (1998). Atmospheric circulation patterns and spatial climatic variations in Beringia. *International Journal of Climatology*, 18(10), 1085–1104. [https://doi.org/10.1002/\(SICI\)1097-0088\(199808\)18:10<1085::AID-JOC305>3.0.CO;2-K](https://doi.org/10.1002/(SICI)1097-0088(199808)18:10<1085::AID-JOC305>3.0.CO;2-K)
- Nagy, N. E., Franceschi, V. R., Solheim, H., Krekling, T., & Christiansen, E. (2000). Wound-induced traumatic resin duct development in stems of Norway spruce (Pinaceae): Anatomy and cytochemical traits. *American Journal of Botany*, 87(3), 302–313. <https://doi.org/10.2307/2656626>
- Neal, E. G., Walter, M. T., & Coffeen, C. (2002). Linking the Pacific Decadal Oscillation to seasonal stream discharge patterns in Southeast Alaska. *Journal of Hydrology*, 263(1–4), 188–197. [https://doi.org/10.1016/S0022-1694\(02\)00058-6](https://doi.org/10.1016/S0022-1694(02)00058-6)
- Newman, M., Alexander, M. A., Ault, T. R., Cobb, K. M., Deser, C., Di Lorenzo, E., et al. (2016). The Pacific Decadal Oscillation, revisited. *Journal of Climate*, 29(12), 4399–4427. <https://doi.org/10.1175/JCLI-D-15-0508.1>
- Nowacki, G. J., and M. G. Kramer (1998), The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska, *Gen. Tech. Rep. PNW-GTR-421*. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 25 p. (Shaw, Charles G., III, tech. coord.; Julin, Kent R., ed.; *Conservation and resource assessments for the Tongass land management plan revision*), 421.
- Nykanen, M.-L., Peltola, H., Quine, C., Kellomäki, S., & Broadgate, M. (1997). Factors affecting snow damage of trees with particular reference to European conditions. *Silva Fennica*, 31(2).
- Orth, D. J. (1967), *Dictionary of Alaska place names*, US Government Printing Office.
- Osterberg, E. C., Winski, D. A., Kreutz, K. J., Wake, C. P., Ferris, D. G., Campbell, S., et al. (2017). The 1200 year composite ice core record of Aleutian Low intensification. *Geophysical Research Letters*, 44, 7447–7454. <https://doi.org/10.1002/2017GL073697>
- Overland, J. E., Adams, J. M., & Bond, N. A. (1999). Decadal variability of the Aleutian low and its relation to high-latitude circulation. *Journal of Climate*, 12(5), 1542–1548. [https://doi.org/10.1175/1520-0442\(1999\)012<1542:DVOTAL>2.0.CO;2](https://doi.org/10.1175/1520-0442(1999)012<1542:DVOTAL>2.0.CO;2)
- Payette, S., Delwaide, A., Morneau, C., & Lavoie, C. (1994). Stem analysis of a long-lived black spruce clone at treeline. *Arctic and Alpine Research*, 26(1), 56–59. <https://doi.org/10.2307/1551877>
- Payette, S., Delwaide, A., Morneau, C., & Lavoie, C. (1996). Patterns of tree stem decline along a snow-drift gradient at treeline: A case study using stem analysis. *Canadian Journal of Botany*, 74(11), 1671–1683. <https://doi.org/10.1139/b96-203>
- Payette, S., Fillion, L., Delwaide, A., & Bégin, C. (1989). Reconstruction of tree-line vegetation response to long-term climate change. *Nature*, 341(6241), 429–432. <https://doi.org/10.1038/341429a0>
- Penhallow, D. P. (1907). *Manual of the North American gymnosperms*. Ginn.
- Pereg, D., & Payette, S. (1998). Development of black spruce growth forms at treeline. *Plant Ecology*, 138(2), 137–147. <https://doi.org/10.1023/A:1009756707596>
- Peterson, D. W., & Peterson, D. L. (2001). Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology*, 82(12), 3330–3345. [https://doi.org/10.1890/0012-9658\(2001\)082\[3330:MHGRTC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3330:MHGRTC]2.0.CO;2)
- Petty, J. A., & Worrell, R. (1981). Stability of coniferous tree stems in relation to damage by snow. *Forestry: An International Journal of Forest Research*, 54(2), 115–128. <https://doi.org/10.1093/forestry/54.2.115>
- Phillips, M. A., & Croteau, R. B. (1999). Resin-based defenses in conifers. *Trends in Plant Science*, 4(5), 184–190. [https://doi.org/10.1016/S1360-1385\(99\)01401-6](https://doi.org/10.1016/S1360-1385(99)01401-6)
- Rodionov, S. N. (2004). A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters*, 31, L09204. <https://doi.org/10.1029/2004GL019448>
- Rodionov, S. N., Bond, N. A., & Overland, J. E. (2007). The Aleutian Low, storm tracks, and winter climate variability in the Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(23–26), 2560–2577. <https://doi.org/10.1016/j.dsr2.2007.08.002>
- Schläpky, R., Jomelli, V., Eckert, N., Stoffel, M., Grancher, D., Brunstein, D., et al. (2016). Can we infer avalanche–climate relations using tree-ring data? Case studies in the French Alps. *Regional Environmental Change*, 16(3), 629–642. <https://doi.org/10.1007/s10113-015-0823-0>
- Schmidt, R. A., & Gluns, D. R. (1991). Snowfall interception on branches of three conifer species. *Canadian Journal of Forest Research*, 21(8), 1262–1269. <https://doi.org/10.1139/x91-176>
- Schneuwly, D. M., Stoffel, M., & Bollschweiler, M. (2009). Formation and spread of callus tissue and tangential rows of resin ducts in Larix decidua and Picea abies following rockfall impacts. *Tree Physiology*, 29(2), 281–289. <https://doi.org/10.1093/treephys/tpn026>
- Schneuwly, D. M., Stoffel, M., Dorren, L. K., & Berger, F. (2009). Three-dimensional analysis of the anatomical growth response of European conifers to mechanical disturbance. *Tree Physiology*, 29(10), 1247–1257. <https://doi.org/10.1093/treephys/tpp056>
- Schweingruber, F. H. (2007). *Wood structure and environment*. Springer Science and Business Media.
- Schweingruber, F. H. (2012). *Trees and wood in dendrochronology: Morphological, anatomical, and tree-ring analytical characteristics of trees frequently used in dendrochronology*. Springer, Verlag. <https://doi.org/10.1007/978-3-642-77157-6>

- Seager, R., Hoerling, M., Schubert, S., Wang, H., Lyon, B., Kumar, A., et al. (2015). Causes of the 2011–14 California drought. *Journal of Climate*, 28(18), 6997–7024. <https://doi.org/10.1175/JCLI-D-14-00860.1>
- Smith, K. T., & Shortle, W. C. (2003). Radial growth of hardwoods following the 1998 ice storm in New Hampshire and Maine. *Canadian Journal of Forest Research*, 33(2), 325–329. <https://doi.org/10.1139/x02-185>
- Sorg, A., Kääb, A., Roesch, A., Bigler, C., & Stoffel, M. (2015). Contrasting responses of Central Asian rock glaciers to global warming. *Scientific Reports*, 5(1), 8228. <https://doi.org/10.1038/srep08228>
- Spatz, H. C., & Bruechert, F. (2000). Basic biomechanics of self-supporting plants: Wind loads and gravitational loads on a Norway spruce tree. *Forest Ecology and Management*, 135(1–3), 33–44. [https://doi.org/10.1016/S0378-1127\(00\)00296-6](https://doi.org/10.1016/S0378-1127(00)00296-6)
- Stathers, R. J., Rollerson, T. P., & Mitchell, S. J. (1994). *Windthrow Handbook for British Columbia Forests*. Victoria: BC Min. For.
- Stoffel, M. (2008). Dating past geomorphic processes with tangential rows of traumatic resin ducts. *Dendrochronologia*, 26(1), 53–60. <https://doi.org/10.1016/j.dendro.2007.06.002>
- Stoffel, M., & Bollschweiler, M. (2009). What tree rings can tell about earth-surface processes: Teaching the principles of dendrogeomorphology. *Geography Compass*, 3(3), 1013–1037. <https://doi.org/10.1111/j.1749-8198.2009.00223.x>
- Stoffel, M., Bollschweiler, M., & Hassler, G. R. (2006). Differentiating past events on a cone influenced by debris-flow and snow avalanche activity—A dendrogeomorphological approach. *Earth Surface Processes and Landforms*, 31(11), 1424–1437.
- Stoffel, M., & Corona, C. (2014). Dendroecological dating of geomorphic disturbance in trees. *Tree-Ring Research*, 70(1), 3–20. <https://doi.org/10.3959/1536-1098-70.1.3>
- Stoffel, M., & Hitz, O. M. (2008). Rockfall and snow avalanche impacts leave different anatomical signatures in tree rings of juvenile Larix decidua. *Tree Physiology*, 28(11), 1713–1720. <https://doi.org/10.1093/treephys/28.11.1713>
- Stoffel, M., & Perret, S. (2006). Reconstructing past rockfall activity with tree rings: Some methodological considerations. *Dendrochronologia*, 24(1), 1–15. <https://doi.org/10.1016/j.dendro.2006.04.001>
- Stoffel, M., Schneuwly, D., Bollschweiler, M., Lievre, I., Delaloye, R., Myint, M., & Monbaron, M. (2005). Analyzing rockfall activity (1600–2002) in a protection forest—A case study using dendrogeomorphology. *Geomorphology*, 68(3–4), 224–241. <https://doi.org/10.1016/j.geomorph.2004.11.017>
- Stokes, A. (1999). Strain distribution during anchorage failure of Pinus pinaster Ait. at different ages and tree growth response to wind-induced root movement. *Plant and Soil*, 217(1/2), 17–27. <https://doi.org/10.1023/A:1004613126353>
- Stokes, M. A. (1996). *An introduction to tree-ring dating*. University of Arizona Press.
- Tape, K. D., Lord, R., Marshall, H.-P., & Ruess, R. W. (2010). Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. *Ecoscience*, 17(2), 186–193. <https://doi.org/10.2980/17-2-3323>
- Torrence, C., & Compo, G. P. (1998). A practical guide to wavelet analysis. *Bulletin of the American Meteorological Society*, 79(1), 61–78. [https://doi.org/10.1175/1520-0477\(1998\)079<0061:APGTWA>2.0.CO;2](https://doi.org/10.1175/1520-0477(1998)079<0061:APGTWA>2.0.CO;2)
- Tremblay, J., & Bégin, Y. (2005). The effects of snow packing on tree growth forms on an island in a recently created reservoir in northern Quebec, Canada. *Ecoscience*, 12(4), 530–539. <https://doi.org/10.2980/11195-6860-12-4-530.1>
- Trenberth, K. E., & Hurrell, J. W. (1994). Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics*, 9(6), 303–319. <https://doi.org/10.1007/BF00204745>
- Ugolini, F. C., & Mann, D. H. (1979). Biopedological origin of peatlands in South East Alaska. *Nature*, 281(5730), 366–368. <https://doi.org/10.1038/281366a0>
- Wade, J. E., & Hewson, E. W. (1979). Trees as a local climatic wind indicator. *Journal of Applied Meteorology*, 18(9), 1182–1187. [https://doi.org/10.1175/1520-0450\(1979\)018<1182:TAALCW>2.0.CO;2](https://doi.org/10.1175/1520-0450(1979)018<1182:TAALCW>2.0.CO;2)
- Walsh, J. E., Overland, J. E., Groisman, P. Y., & Rudolf, B. (2011). Ongoing climate change in the Arctic. *Ambio*, 40(S1), 6–16. <https://doi.org/10.1007/s13280-011-0211-z>
- Warrillow, M., & Mou, P. (1999). Ice storm damage to forest tree species in the ridge and valley region of southwestern Virginia. *Journal of the Torrey Botanical Society*, 126(2), 147–158. <https://doi.org/10.2307/2997291>
- Wendler, G., Galloway, K., & Stuefer, M. (2016). On the climate and climate change of Sitka, Southeast Alaska. *Theoretical and Applied Climatology*, 126(1–2), 27–34. <https://doi.org/10.1007/s00704-015-1542-7>
- Westing, A. H. (1965). Formation and function of compression wood in gymnosperms. *The Botanical Review*, 31(3), 381–480. <https://doi.org/10.1007/BF02859131>
- Wiles, G. C., D'Arrigo, R. D., Barclay, D., Wilson, R. S., Jarvis, S. K., Vargo, L., & Frank, D. (2014). Surface air temperature variability reconstructed with tree rings for the Gulf of Alaska over the past 1200 years. *The Holocene*, 24(2), 198–208. <https://doi.org/10.1177/0959683613516815>
- Wilson, R., Anchukaitis, K., Briffa, K. R., Büntgen, U., Cook, E., D'Arrigo, R., et al. (2016). Last millennium northern hemisphere summer temperatures from tree rings: Part I: The long term context. *Quaternary Science Reviews*, 134(1), 1–18. <https://doi.org/10.1016/j.quascirev.2015.12.005>
- Wilson, R., Wiles, G., D'Arrigo, R., & Zweck, C. (2007). Cycles and shifts: 1,300 years of multi-decadal temperature variability in the Gulf of Alaska. *Climate Dynamics*, 28(4), 425–440. <https://doi.org/10.1007/s00382-006-0194-9>
- Winski, D., Osterberg, E., Ferris, D., Kreutz, K., Wake, C., Campbell, S., et al. (2017). Industrial-age doubling of snow accumulation in the Alaska Range linked to tropical ocean warming. *Scientific Reports*, 7(1), 17,869. <https://doi.org/10.1038/s41598-017-18022-5>
- Wise, E. K. (2016). Five centuries of US West Coast drought: Occurrence, spatial distribution, and associated atmospheric circulation patterns. *Geophysical Research Letters*, 43, 4539–4546. <https://doi.org/10.1002/2016GL068487>
- Wise, E. K., & Dannenberg, M. P. (2014). Persistence of pressure patterns over North America and the North Pacific since AD 1500. *Nature Communications*, 5(1), 4912. <https://doi.org/10.1038/ncomms5912>
- Woodridge, G. L., Musselman, R. C., Sommerfeld, R. A., Fox, D. G., & Connell, B. H. (1996). Mean wind patterns and snow depths in an alpine-subalpine ecosystem as measured by damage to coniferous trees. *Journal of Applied Ecology*, 33(1), 100–108. <https://doi.org/10.2307/2405019>
- Wu, H., & Hu, Z. H. (1997). Comparative anatomy of resin ducts of the Pinaceae. *Trees*, 11(3), 135–143. <https://doi.org/10.1007/s004680050069>
- Zaginaev, V., Ballesteros-Cánovas, J. A., Erokhin, S., Matov, E., Petrakov, D., & Stoffel, M. (2016). Reconstruction of glacial lake outburst floods in northern Tien Shan: Implications for hazard assessment. *Geomorphology*, 269, 75–84. <https://doi.org/10.1016/j.geomorph.2016.06.028>
- Zhu, X., Sun, J., Liu, Z., Liu, Q., & Martin, J. E. (2007). A synoptic analysis of the interannual variability of winter cyclone activity in the Aleutian low region. *Journal of Climate*, 20(8), 1523–1538. <https://doi.org/10.1175/JCLI4077.1>
- Zona, S. (2004). Plant resins: Chemistry, evolution, ecology, Ethnobotany by Jean H. Langenheim. *Systematic Botany*, 29(1), 222.

Erratum

In the originally published version of this article, the correlations in Figures 7b and 7c were erroneously switched with one another. The figure has since been corrected, and this version may be considered the authoritative version of record.